Evaluation of Funnel Traps for Characterizing the Bark Beetle (Coleoptera: Scolytidae) Communities in Ponderosa Pine Forests of North-Central Arizona

Christopher J. Hayes,[1,2] Tom E. DeGomez,[1] Karen M. Clancy,[3] Kelly K. Williams,[1] Joel D. McMillin,[4] and John A. Anhold[4]

ABSTRACT Lindgren funnel traps baited with aggregation pheromones are widely used to monitor and manage populations of economically important bark beetles (Coleoptera: Scolytidae). This study was designed to advance our understanding of how funnel trap catches assess bark beetle communities and relative abundance of individual species. In the second year (2005) of a 3-yr study of the bark beetle community structure in north-central Arizona pine (*Pinus* spp.) forests, we collected data on stand structure, site conditions, and local bark beetle-induced tree mortality at each trap site. We also collected samples of bark from infested (brood) trees near trap sites to identify and determine the population density of bark beetles that were attacking ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, in the area surrounding the traps. Multiple regression models indicated that the number of *Dendroctonus* and *Ips* beetles captured in 2005 was inversely related to elevation of the trap site, and positively associated with the amount of ponderosa pine in the stand surrounding the site. Traps located closer to brood trees also captured more beetles. The relationship between trap catches and host tree mortality was weak and inconsistent in forest stands surrounding the funnel traps, suggesting that trap catches do not provide a good estimate of local beetle-induced tree mortality. However, pheromone-baited funnel trap data and data from gallery identification in bark samples produced statistically similar relative abundance profiles for the five species of bark beetles that we examined, indicating that funnel trap data provided a good assessment of species presence and relative abundance.

KEY WORDS *Dendroctonus*, *Ips*, multiple regression models, *Pinus ponderosa*, stand characteristics

Lindgren funnel traps baited with aggregation pheromones (Lindgren 1983) (hereafter referred to as funnel traps) are widely used to monitor and suppress populations of economically important bark beetles (Coleoptera: Scolytidae). For example, recent articles by Bentz (2006) and Hansen et al. (2006) list many uses of funnel traps for research, including detecting the presence of particular species of bark beetles, monitoring spatial and temporal patterns of adult flight, forecasting infestation trends, as well as numerous applications associated with suppression strategies. However, they also emphasized the need for more information on how useful funnel trap catch data are for estimating adult emergence and flight periodicity (Bentz 2006), or beetle population levels and host tree mortality (Hansen et al. 2006). In addition, Hansen et al. (2006) noted that funnel trap catches can be affected by many factors linked to local site conditions such as topography, the density and composition of the stand, the direction and strength of wind, and temperature. Moreover, Fettig et al. (2007) have documented that bark beetle-caused tree mortality is frequently related to certain forest stand conditions and site characteristics.

Bark beetle-caused mortality of ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, in the southwestern United States has been relatively low over the last century, but a drought-induced outbreak from 2001 to 2003 (USDA 2004, 2005; Gaylord et al. 2006; Parker et al. 2006) has renewed interest in the biology, ecology, and management of these insects in this region. Early in the outbreak, *Ips* species [e.g., *I. lecontei* Swaine and *I. pini* (Say)] were the primary tree-killing species, in particular at low to mid-elevations, whereas *Dendroctonus* species (e.g., *D. brevicomis* LeConte, *D. adjunctus* Blandford, and *D. frontalis* Zimmermann) became increasingly important later in the outbreak at mid- to high elevations (USDA 2005; J.D.M., unpublished data). Ponderosa pine trees were observed frequently

[1] School of Natural Resources, University of Arizona, NAU Box 15018, Flagstaff, AZ 86011.
[2] Corresponding author, e-mail: chayes@email.arizona.edu.
[3] USDA–Forest Service Research and Development, Rocky Mountain Research Station, 2500 S. Pine Knoll Dr., Flagstaff, AZ 86001-6381.
[4] USDA–Forest Service, Southwestern Region, Forestry and Forest Health, Arizona Zone, 2500 S. Pine Knoll Dr., Flagstaff, AZ 86001-6381.

to be under attack by a complex of species during this outbreak (USDA 2005; J.D.M., unpublished data). Ponderosa pine mortality approached 100% in some stands on the Coconino National Forest (Gitlin et al. 2006), but it averaged ≈12.5% across the entire national forest between 2001 and 2004 (J.D.M., unpublished data). Elevation, tree density, and slope were all significant variables in logistic regression models for estimating the probability of occurrence of mortality in ponderosa pine stands on the Coconino National Forest (J.D.M., unpublished data).

The purpose of our study was to help advance the understanding of the meaning of funnel trap catches to improve methods to predict where, when, and how much bark beetle activity will occur in forests. In 2004, we initiated a 3-yr beetle trapping study in north-central Arizona to determine whether there are elevational differences in the community structure of bark beetles that attack ponderosa pines (Williams et al. 2008). We expanded this study in 2005 by collecting data on stand structure, site conditions, and local bark beetle-induced tree mortality at each funnel trap site. We also quantified the percentage of phloem used by different bark beetle species from infested trees near the trap sites to identify and determine the relative population density of the species that were attacking ponderosa pines in the area surrounding the traps.

There were four objectives of our study. The first was to investigate relationships between the number of bark beetles captured in our funnel traps in 2005 and the stand conditions and site attributes where the funnel traps were located. The second was to evaluate the effect that distance from the funnel trap to the nearest brood tree (i.e., a ponderosa pine tree under attack by bark beetles in 2005) had on trap catches. Brood trees in the vicinity of a trap could provide nearby sources of bark beetles and pheromones and thus increase trap catches, or they could compete for beetles in flight and thus decrease trap catches. Brood trees close to a trap can also indicate spillover to neighboring trees from the baited traps (Borden 1989, Laidlaw et al. 2003). The third objective was to investigate whether larger trap catches were associated with increased levels of local bark beetle-induced tree mortality in 2005. In other words, do trap catch levels reflect bark beetle-caused tree mortality levels in stands surrounding traps? The fourth objective was to compare funnel trap data to results from bark samples collected from infested trees to better understand the utility of funnel traps for characterizing the actual presence and relative abundance of various species of bark beetles in species-rich ecosystems such as the ponderosa pine forests in the southwestern United States.

Materials and Methods

Site Locations. The 2004–2006 elevational gradient study included 10 funnel trap sites in each of three elevation bands (high, ≈2,500–2,700 m; mid, ≈2,050–2,250 m; and low, ≈1,600–1,750 m) that covered most of the elevational range of ponderosa pine in north-central Arizona (Williams et al. 2008). The 30 sites were established in stands of ponderosa pine in north-central Arizona in spring 2004; they were located within 100 m of the edge of ponderosa pine stands that had low to high densities of bark beetle-killed trees. Traps were placed within 50–200 m of U.S. Forest Service roads with ≥2-km spacing between trap sites.

We used 26 of the 30 trap sites in this study (Table 1). Four sites were excluded because we could not collect the necessary associated stand data. Two of the 10 low-elevation sites were not used because they were damaged in fires, whereas two of the 10 high-elevation sites were not accessible in fall 2004 and thus were eliminated.

Pheromone-Baited Funnel Trap Sampling. One cluster of three 12-unit funnel traps was deployed at each of the eight or 10 sites per elevational band. Traps were arranged in an equilateral triangle, with ≈15 m between traps (Fig. 1). The middle of the triangle served as the plot center. One of the funnel traps was baited with a lure designed to attract *Ips pini* [lanierone, 4-mg bubble cap release device, release rate 0.009 mg/d at 25°C; 97% (−)-ipsdienol, 40-mg bubble cap release device, release rate 0.2 mg/d at 25°C]. The second trap was baited with a lure for *I. lecontei* [50% (−)-ipsdienol, 40-mg bubble cap release device, release rate 0.2 mg/d at 25°C; 50% (−)-ipsenol, 40-mg bubble cap release device, release rate 0.4 mg/d at 25°C; 83% (−)-*cis*-verbenol, 60-mg bubble cap release device, release rate 0.3–0.6 mg/d at 25–30°C], and the third with a lure for *D. brevicomis* [50% (−)-frontalin, 400-μl Eppendorf tube, release rate 2.8 mg/d at 20°C; 50% (−)-*exo*-brevicomin, 250-μl Eppendorf tube, release rate 0.5 mg/d at 20°C; myrcene, 2- by 1.8-ml Eppendorf tubes, release rate 5.5 mg/d each at 20°C]. Our objective was not to test the relative efficacy of each lure; therefore, the catches of three funnel traps were pooled for each site. To ensure their effectiveness, lures were replaced (and rotated within clusters) every 49 d, a much shorter period than the 90 d recommended by the manufacturer (Pherotech International Inc., Delta, BC, Canada). Limitations on site access due to snow and road closures caused trap deployment dates to vary across elevation bands. Trap collection occurred from 8 March to 6 December 2005 at low-elevation sites, from 23 March to 8 December 2005 at mid-elevation sites, and from 25 April to 28 November 2005 at high-elevation sites. Traps were baited 7 d before first collection. Trap contents were collected approximately once a week and captured beetles were identified and tallied in the laboratory (Williams et al. 2008). Voucher specimens are maintained at the Rocky Mountain Research Station, USDA–Forest Service, Flagstaff, AZ.

Weekly mean trap catches for the trapping season were calculated for each bark beetle species at each trap site beginning when traps were placed at the site and bark beetle flight started, and ending the week before two consecutive weeks of no beetle catches or when inclement weather dictated trap breakdown. Beetle flight season length varied from 40 wk at some low-elevation sites (from 8 March to 6 December) to

Table 1.   Locations of the 26 funnel trap sites to collect bark beetles in ponderosa pine stands of north-central Arizona, Coconino and Gila counties, 2004–2005

Site label	National Forest	Latitude	Longitude	Elevation		Used in $n = 16$ data set[a]
				m	Band	
HCRO	Coconino	35° 23′ N	111° 50′ W	2,507.6	High	Yes
HFRE	Coconino	35° 17′ N	111° 41′ W	2,564.9	High	Yes
HMOS	Coconino	34° 57′ N	111° 31′ W	2,519.8	High	Yes
HMOT	Coconino	34° 58′ N	111° 30′ W	2,559.5	High	No
HNEW	Kaibab	35° 23′ N	111° 52′ W	2,532.9	High	No
HORI	Coconino	35° 17′ N	111° 39′ W	2,627.7	High	Yes
HVIE	Coconino	35° 18′ N	111° 43′ W	2,650.9	High	Yes
HWAT	Coconino	35° 17′ N	111° 37′ W	2,505.2	High	Yes
LCHR	Tonto	34° 18′ N	111° 03′ W	1,735.1	Low	Yes
LCON	Tonto	34° 21′ N	111° 25′ W	1,717.1	Low	Yes
LHCA	Tonto	34° 14′ N	110° 58′ W	1,707.6	Low	No
LHCR	Tonto	34° 13′ N	110° 58′ W	1,619.5	Low	Yes
LMAR	Tonto	34° 09′ N	110° 58′ W	1,637.8	Low	Yes
LMOO	Tonto	34° 21′ N	111° 13′ W	1,735.7	Low	No
LSHA	Tonto	34° 23′ N	111° 17′ W	1,633.2	Low	No
LWEB	Tonto	34° 23′ N	111° 21′ W	1,600.6	Low	Yes
MASH	Coconino	35° 01′ N	111° 26′ W	2,164.0	Mid	Yes
MCIN	Coconino	35° 20′ N	111° 32′ W	2,146.3	Mid	No
MCOW	Coconino	34° 53′ N	111° 26′ W	2,230.0	Mid	Yes
MMAR	Coconino	35° 06′ N	111° 32′ W	2,195.7	Mid	Yes
MMOL	Coconino	34° 59′ N	111° 27′ W	2,201.2	Mid	No
MRIM	Coconino	34° 28′ N	111° 28′ W	2,117.0	Mid	Yes
MSCH	Coconino	35° 14′ N	111° 39′ W	2,194.2	Mid	No
MSUN	Coconino	35° 22′ N	111° 33′ W	2,155.2	Mid	No
MTUR	Coconino	35° 13′ N	111° 31′ W	2,090.2	Mid	Yes
MWAL	Coconino	35° 10′ N	111° 31′ W	2,058.2	Mid	No

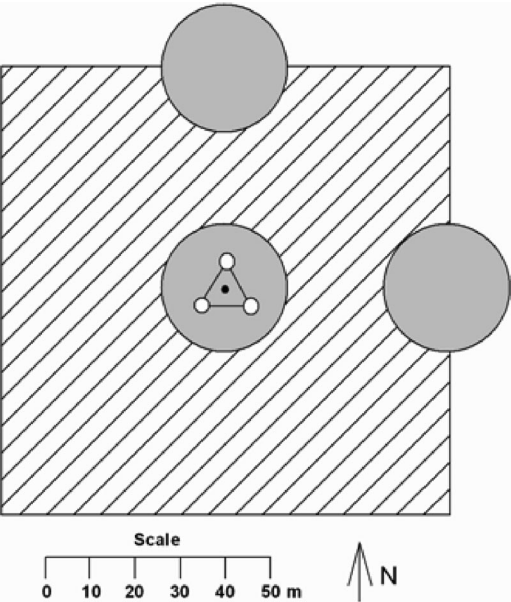[a] This data set was based on sites that had a brood tree within 200 m of traps.

Fig. 1.   Diagram (drawn approximately to scale) showing the configuration of each trap site and the plots used to sample stand characteristics in the area near the traps. The plot center is marked with the black dot; the triangle and the small white circles show the placement of the three 12-unit funnel traps. The larger gray circles represent the three circular fixed area (1/20-ha) plots used to measure stand characteristics. The hatched area indicates the square fixed area (1-ha) plot, which delimits the area where data were collected from brood trees.

25 wk at some high-elevation sites (from 23 May to 8 November).

Species caught in traps and used as dependent variables in this study included five species of *Ips* and five species of *Dendroctonus* (Table 2). The weekly mean trap catches for all 10 species were pooled for each trap site and analyzed as another dependent variable

Table 2.   Response of bark beetles to pheromone-baited funnel traps compared with presence in bark samples from infested ponderosa pine trees near the trap sites

Bark beetle species captured in funnel traps		Presence or absence in bark samples collected from various bole ht[a]			
Genus	Species	1 m	3 m	5 m	7 m[b]
Dendroctonus	*D. adjunctus* Blandford	X	X	X	X
	D. approximatus Dietz	X	X	−	−
	D. brevicomis LeConte	X	X	X	X
	D. frontalis Zimmermann	X	X	X	X
	D. valens LeConte	−	−	−	−
Ips	*I. calligraphus* (Germar)	X	X	−	X
	I. knausi Swaine	X	X	X	X
	Other *Ips* species[c]	X[d]	X	X	X
	I. latidens (LeConte)				
	I. lecontei Swaine				
	I. pini (Say)				

[a] Presence (X) or absence (−) of galleries of bark beetle species in bark samples collected from various bole heights (meters above the ground).
[b] Seven meters was never >60% of the total height of the tree.
[c] Galleries of *I. latidens, I. lecontei,* and *I. pini* could not be identified to the species level, so these three *Ips* species were pooled.
[d] "Other *Ips* species" galleries were found at the 1-m bole height in only one of 13 trees sampled.

(all species). We also pooled and used a subset of four species, determined a priori, that we hypothesized were important contributors to bark beetle-caused mortality in ponderosa pine in north-central Arizona during this drought event (i.e., drought-initiated outbreak that lasted ≈2002 through 2004). The weekly mean trap catches for *I. lecontei*, *I. pini*, *D. brevicomis*, and *D. frontalis* composed this second composite dependent variable (principal tree-killers).

Characterization of Stand Conditions and Site Attributes. Systematic sampling within sites was used to obtain independent variable data on stand structure and site conditions in the fall of 2004. Three circular, fixed area (1/20 ha) plots were established at each site, including one at the plot center, one 50 m north of the plot center, and one 50 m east of the plot center (Fig. 1). We measured diameter at breast height (dbh) (1.37 m above the ground); condition class (live, bark beetle-killed, and nonbeetle-killed snags); and species of all live and dead trees on the plots, and elevation, slope, and aspect of the site. The information on live trees was used to calculate stand basal area (m²/ha), ponderosa pine basal area, percentage of stand basal area that was ponderosa pine, number of trees per ha, number of ponderosa pine trees per ha, mean dbh of ponderosa pine trees, and stand density index.

Brood Tree Plots. We established brood tree plots at each trap site to collect additional independent variable data on ponderosa pine trees under attack that could be nearby sources of bark beetles captured in the funnel traps; this information could also indicate the amount of local bark beetle-induced tree mortality in 2005. In spring and fall 2005, these fixed area (1-ha) square plots were used to record data on bark beetle-attacked ponderosa pines (Fig. 1). All ponderosa pine trees >12.7 cm dbh that were under attack (as indicated by pitch tubes or boring dust) or recently killed by bark beetles were categorized as either: 1) a fader (needles were a faded green/yellow to orange color) that had been successfully attacked by bark beetles in 2005; 2) a recently dead tree that had been attacked and killed by bark beetles in 2004 (orange needles were retained on <50% of the original crown); or 3) a green tree that had been mass attacked (>10 successful attacks) by bark beetles in 2005, but they had not yet faded. DBH and azimuth and distance from the plot center, were recorded for each of these trees. Low-elevation plots were measured 21–24 February 2005; mid- and high-elevation plots were measured between 4 April and 25 May 2005. Plots were remeasured 7 September through the end of October 2005.

So as to only reflect 2005 bark beetle activity, data from brood trees in category 1 (fader) or 3 (green mass attacked) were used to calculate the basal area of bark beetle brood trees and the distance from the plot center to the nearest brood tree. The "basal area of bark beetle brood trees" was calculated by using both spring and fall data, and "distance from the plot center to the nearest brood tree" was determined by using fall data. Ten of the 26 trap sites did not have any category 1 or three brood trees within 50 m of the plot center, so the data for the variable "distance from plot

center to nearest brood tree" was missing for these sites. Consequently, we used a smaller data set ($n = 16$ sites) for analyses that included this independent variable (Table 1).

Bark Samples. We collected samples of bark from beetle-infested trees near the funnel trap sites so that we could identify the beetle galleries and thereby 1) establish which species were attacking ponderosa pines in the area surrounding the traps and 2) estimate their relative population densities (Table 2). At each trap site, we looked for a ponderosa pine brood tree (i.e., a tree attacked and killed by bark beetles in 2005) that was within a 200-m radius of the plot center and had a dbh of 20–60 cm. There were 13 sites with brood trees that met our criteria—seven were high-elevation sites, three were mid-elevation sites, and three were low-elevation sites. In total, 52 bark samples (each 1,000 cm²) were removed from the north aspect of these 13 trees at 1, 3, 5, and 7 m above the ground (13 trees × 4 samples/tree = 52) from September through October, 2005. Galleries characteristic of *Dendroctonus* and *Ips* were identified to the species level, if possible, and the percentage of the gallery area within each bark sample occupied by each bark beetle species was estimated visually. Gallery lengths could not be measured accurately because of damage to the phloem from wood borers and fungi. We could not distinguish among the galleries made by *I. latidens* (LeConte), *I. lecontei*, and *I. pini*, so data from these three *Ips* species were pooled. Galleries of *Dendroctonus* species were identified by using egg gallery and larval mine characteristics. *D. frontalis* and *D. brevicomis* galleries can be grouped by egg gallery width and sinuosity, as can *D. adjunctus* and *D. approximatus* Dietz. Further identification to the species level was accomplished with relatively high confidence by using larval mine characteristics; *D. frontalis* constructs pupal chambers in the phloem, visible on the inner bark surface, whereas *D. brevicomis* constructs pupal chambers in the outer bark, and they are not observed on the inner bark surface.

We used these data to develop abundance profiles, for each elevation band, for a subset of five species [*D. adjunctus*, *D. approximatus*, *D. brevicomis*, *D. frontalis*, and *I. calligraphus* (Germar)]. All of these species were captured in the pheromone-baited funnel traps and are known to attack the low to mid-bole area of their host trees (Furniss and Carolin 1977), where we collected the bark samples (Table 2). However, only 36 of the 52 samples contained galleries of at least one of the five beetle species. There were $n = 12$ bark samples from the three low-elevation brood trees; $n = 6$ bark samples from the three mid-elevation brood trees; and $n = 18$ bark samples from the seven high-elevation brood trees. For each of these 36 bark samples, we estimated the gallery area occupied by each species identified relative to the total area occupied by the five beetle species listed above.

The funnel trap data were used to develop parallel abundance profiles for this same subset of five species. The relative abundance profiles were based on collections of $n = 11,995$ beetles for the low-elevation

bands, $n = 4,139$ beetles for the mid-elevation bands, and $n = 4,606$ beetles for the high-elevation bands.

Statistical Analyses. *Relating Bark Beetle Trap Catches to Stand and Site Characteristics and Host Tree Mortality.* First, we used correlation analysis to investigate associations between stand-level characteristics and bark beetle trap catches. Pearson product moment correlation coefficients (r) were calculated between stand characteristics and the number of bark beetles captured for all 10 bark beetle species pooled ("All species") (Table 2) and for the subset of four "Principal tree-killers." We also used all *Dendroctonus* and all *Ips* species pooled as two additional bark beetle variables to ensure a comprehensive inspection of the data set. The following 11 stand and site variables were assessed: 1) elevation of the trap site; 2) basal area of the stand; 3) of ponderosa pine trees, and of bark beetle brood trees in the spring (4) and fall (5) of 2005 (indicative of the amount of local bark-beetle induced tree mortality in 2005); 6) percentage of stand basal area that was ponderosa pine; 7) number of trees/ha; 8) number of ponderosa pine trees per ha; 9) mean dbh of ponderosa pine trees; 10) stand density index; and 11) distance from the plot center to the nearest brood tree.

We used the results from the correlation analyses to help select a subset of independent variables to draw on for developing multiple regression models to predict the mean weekly trap catches. Two dependent variables were used: "All (10) species" of bark beetles captured, and the four species of "Principal tree-killers." Based on detectable correlations between the number of bark beetles trapped and independent variables, four of the 11 site and stand independent variables (elevation, basal area of ponderosa pine, percentage of stand basal area that was ponderosa pine, and distance from the plot center to the nearest brood tree) were considered for multiple regression models. In addition, we decided to include the fall 2005 measure of basal area of brood trees in our regression models because it was the best gauge that we had of host tree mortality. Because investigating potential relationships between trap catch data and beetle-induced tree mortality was one of our main objectives, we felt that we should further investigate any effects this variable may have, in the context of a multivariate regression model, despite the lack of any detectable correlation with bark beetles trapped. Data for the independent variable of interest, "distance from the plot center to the nearest brood tree," was missing for 10 of the trap sites (i.e., there were no brood trees within 200 m, so distance to nearest brood tree was not known). Consequently, we developed additional models based on data from the 16 trap sites (see Table 1, $n = 16$ data set) that included this variable.

Independent variables under consideration for entrance into models were examined by using best subset regression models (Analytical Software 2000). A model with a minimal number of independent variables and a high adjusted R^2 value was selected for additional best subset testing with the addition of all the possible squared and interaction terms for the

independent variables. The same criteria (minimal number of independent variables, high adjusted R^2 value) were used to choose the best model. This model was subsequently evaluated by using stepwise regression, with P to enter and exit the model set at 0.05 to ensure that all the independent variables included in the final regression model were significant (i.e., partial P values ≤ 0.05) (Analytical Software 2000). Plots of the standardized residuals were used to determine whether the fit of the models was appropriate.

The equations for the final regression models were used to generate response surfaces that displayed how the mean trap catches were related to different values of two independent variables considered simultaneously. The resulting three-dimensional graphs showed the predicted number of bark beetles trapped (on the vertical z-axis) as a function of two independent variables on the x- and y-axes, respectively. We limited the minimum and maximum values graphed for the x- and y-axes to the approximate range of observed values for the corresponding independent variables. Nonetheless, some of the predicted values of the number of bark beetles trapped (on the z-axis) were <0 or much larger than the maximum observed value.

Comparing Two Measures of Bark Beetle Relative Abundance. We compared the relative abundance of five species of bark beetles across the three elevation bands as determined from 1) funnel trap catches versus 2) the percentage area of galleries in the bark samples collected from nearby brood trees. We used the Multiresponse blocked permutations procedure (MRBP, a nonparametric procedure based on Euclidian distance, performed with Microsoft Excel macros developed by Rudy King, USDA–Forest Service, Rocky Mountain Research Station, Statistics Unit) to test the null hypothesis that there were no differences between the two measures. This is a modification of a multiresponse permutation procedure (Mielke and Berry 2001). The MRBP analysis was performed by comparing the relative abundance profiles (percentage of the total for each species) of the two sampling methods.

Results

Relationship of Bark Beetle Trap Catches to Stand and Site Characteristics and Host Tree Mortality. There were significant ($P \leq 0.05$) Pearson correlation coefficients (r) between the number of "All species" of bark beetles captured in funnel traps and elevation of the trap site, ponderosa pine basal area, percentage of ponderosa pine basal area, and distance from the plot center to the nearest brood tree (Table 3). Consequently, we considered these four independent variables and fall 2005 brood tree basal area for inclusion in our multiple regression models. We excluded the other six stand characteristics that did not have significant correlations with numbers of bark beetles (Table 3).

When *Ips* and *Dendroctonus* were evaluated separately, there were some differences between the two

Table 3. Pearson correlation coefficients (r) between number of bark beetles captured in pheromone-baited funnel traps and forest stand characteristics, north-central Arizona, 2005

Stand characteristic (units)	No. bark beetles trapped in 2005			
	All species	Principal tree killers[a]	*Dendroctonus* spp.	*Ips* spp.
Elevation (m)[b]	−0.458*	−0.654***	−0.230 NS	−0.469*
Ponderosa pine basal area (m²/ha)[b]	0.430*	0.137 NS	0.335 NS	0.295 NS
% Ponderosa pine basal area[b]	0.380*	0.222 NS	0.186 NS	0.395*
Distance from plot center to nearest brood tree (m)[c]	−0.555*	−0.409 NS	−0.588*	−0.189 NS

Significance of r values: *, $P \leq 0.05$; ***, $P \leq 0.001$; NS, $P > 0.05$. There were no significant correlations (i.e., all P values > 0.05) between numbers of bark beetles and the following stand characteristics: basal area (m²/ha) of the stand; basal area of bark beetle brood trees in spring or fall 2005; trees/ha; ponderosa pine trees/ha; stand density index; or average ponderosa pine dbh (cm).

[a] *Ips lecontei, I. pini, D. brevicomis,* and *D. frontalis.*
[b] $n = 26$ trap sites.
[c] $n = 16$ trap sites.

genera (Table 3). *Ips* spp. had a significant inverse relationship with elevation, whereas *Dendroctonus* spp. did not. In contrast, *Dendroctonus* spp. showed a significant inverse relationship with distance from the plot center to the nearest brood tree, but *Ips* spp. did not. Also, *Ips* spp. showed a significant positive relationship with percentage of ponderosa pine basal area, but *Dendroctonus* spp. did not.

The four multiple regression models that we selected for predicting the number of bark beetles captured in our traps included all five of the independent variables considered, but in different combinations of two to four variables (Table 4). The models were all

highly significant ($P < 0.001$), with adjusted R^2 values ranging from 47 to 76%.

Elevation of the trap site was included in all of the models and accounted for more of the variation in the model (based on individual adjusted R^2 values) for the "Principal tree-killers" models (Table 4B and D) compared with the "All species" models (Table 4A and C). The regression coefficient was always negative (Table 4); the inverse relationship between elevation and number of bark beetles trapped is evident in the response surface graphs (Figs. 2, 3A and B, and 4A and B).

The amount of ponderosa pine in the stands surrounding the trap sites was incorporated in three of

Table 4. Four multiple regression models (A–D) relating mean weekly trap catch of bark beetles to elevation of the trap site and various forest stand characteristics, north-central Arizona, 2005

Model	Independent variables (x_n)		Coefficient		Partial P	Model Adj. R^2	Model statistics				
	Variable (units)	Range of values	Mean	SE			F	df	P	R^2	Adj. R^2
A. y = All species of bark beetles ($n = 26$ trap sites[a]) (range of values 0.96–94.92 beetles)											
	Constant	—	94.5700	17.9161	<0.001	—	12.1	2, 23	<0.001	0.5124	0.4700
	x_1 Elevation (m)	1,600.6–2,650.9 m	−0.03353	0.00853	0.001	0.1766					
	x_2 Ponderosa pine basal area (m²/ha)	0.09–38.04 m²/ha	1.11692	0.29555	0.001	0.4700					
B. y = Principal tree-killing bark beetles[b] ($n = 26$ trap sites[a]) (range of values 0.58 −70.63 beetles)											
	Constant	—	83.6573	13.9834	<0.001	—	14.5	2, 23	<0.001	0.5582	0.5198
	x_1 Elevation (m)	1,600.6–2,650.9 m	−0.03354	0.00652	<0.001	0.4045					
	x_2 % Ponderosa pine basal area	0.42–100.00%	0.19684	0.07571	0.016	0.5198					
C. y = All species of bark beetles ($n = 16$ trap sites[c]) (range of values 12.31–94.92 beetles)											
	Constant	—	111.294	19.7749	<0.001	—	10.3	3, 12	0.001	0.7193	0.6491
	x_1 Elevation (m)	1,600.6–2,650.9 m	−0.03496	0.00942	0.003	0.1970					
	x_2 Distance from plot center to nearest brood tree (m)	5.0–49.3 m	−1.07507	0.30480	0.004	0.4251					
	x_3 % Ponderosa pine basal area	10.59–100.00%	0.40604	0.13316	0.010	0.6491					
D. y = Principal tree-killing bark beetles[b] ($n = 16$ trap sites[c]) (range of values 2.38–70.63 beetles)											
	Constant	—	105.843	18.9777	<0.001	—	12.8	4, 11	<0.001	0.8237	0.7595
	x_1 Elevation (m)	1,600.6–2,650.9 m	−0.03654	0.00894	0.002	0.5103					
	x_2 Distance from plot center to nearest brood tree (m)	5.0–49.3 m	−0.68813	0.21529	0.009	0.5962					
	x_3 fall 2005 brood tree Basal area (m²/ha)	0.00–0.97 m²/ha	240.742	95.5996	0.029	0.6815					
	x_4 Elevation × fall 2005 Brood tree basal area	0.00–2548.9	−0.08346	0.03773	0.049	0.7595					

[a] Distribution of trap sites among elevation bands: low, $n = 8$; mid, $n = 10$; and high, $n = 8$.
[b] *Ips lecontei, I. pini, D. brevicomis,* and *D. frontalis.*
[c] Distribution of trap sites among elevation bands: low, $n = 5$; mid, $n = 5$; and high, $n = 6$.

A All species
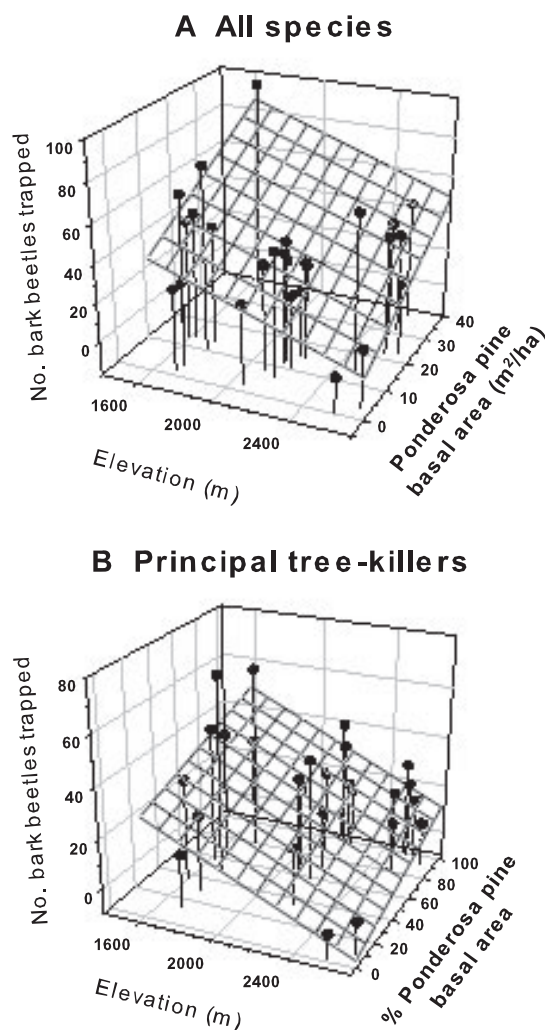

B Principal tree-killers

Fig. 2. Three-dimensional multiple regression response surfaces overlaid on the observed data points (solid circles with lines extending down to the bottom plane of the graph) for mean weekly trap catches of bark beetles at 26 funnel trap sites in north-central Arizona in 2005. (A) Response surface for number of all species of bark beetles to elevation and ponderosa pine basal area (see Table 4A for the model and statistics). (B) Response surface for number of the principal tree-killing bark beetles (*I. lecontei*, *I. pini*. *D. brevicomis*, and *D. frontalis*) to elevation and percentage of ponderosa pine basal area (see Table 4B for the model and statistics).

the four models, as either ponderosa pine basal area (Table 4A) or percentage of ponderosa pine basal area (Table 4B and C). Both of these variables had positive regression coefficients and their inclusion increased the adjusted R^2 values for the models. The response surface graphs show that traps located in stands with a greater basal area of ponderosa pine (Fig. 2A) or a greater percentage of ponderosa pine basal area (Figs. 2B and 3B and C) tended to capture more bark beetles. Traps located in sites with combinations of low elevation and more ponderosa pine caught the most bee-

tles, whereas traps located in sites with combinations of high elevation and less ponderosa pine caught the fewest beetles (Figs. 2 and 3B).

The variable "Distance from the plot center to the nearest brood tree" entered both of the models with the subset of $n = 16$ trap sites (Table 4C and D). Its addition increased the adjusted R^2 values for the models for "All species" more than for the "Principal tree-killers." The regression coefficients were both negative; the response surface graphs illustrate that traps located closer to brood trees captured more beetles (Figs. 3A and C and 4A and C). Traps located in sites with combinations of low elevation and nearby brood trees (Figs. 3A and 4A) or a greater percentage of ponderosa pine basal area and nearby brood trees (Fig. 3C) caught the most beetles.

The variable that measured host tree mortality, "Fall 2005 brood tree basal area," only entered the model for the "Principal tree-killers" when we used the subset of $n = 16$ trap sites (Table 4D). This regression model had the highest adjusted R^2 value ($\approx 76\%$) of the four models that we selected, but it was also the most complex model, with three independent variables (elevation, distance from the plot center to the nearest brood tree, and basal area of brood trees in fall 2005) plus the interaction term of elevation $\times$ fall 2005 brood tree basal area. In combination, brood tree basal area and the interaction term increased the adjusted R^2 value for the model (Table 4D). The regression coefficient for brood tree basal area was positive; the response surface graphs show that sites with a greater basal area of brood trees had higher trap catches (Fig. 4B and C). Trap catches were maximized under combinations of low elevation and proximity of the trap (closer) to the nearest brood tree (Fig. 4A) or combinations of low elevation and high brood tree basal area (Fig. 4B). The negative coefficient for the interaction term (Table 4D) indicates that the positive slope for brood tree basal area is steepest at low elevations and becomes progressively less pronounced as elevation increases (Fig. 4B).

Comparison of the Two Measures of Bark Beetle Relative Abundance. No significant difference was detected between the two measures of pine bark beetle relative abundance (MRBP test statistic $= 0.3671$, $P = 0.167$). Pheromone-baited funnel traps and gallery identification in bark samples produced statistically similar relative abundance profiles for the five target species of bark beetles at each of three elevations (Fig. 5). Because the power of this test was weak (only three sites at each of the low- and mid-elevation bands had trees that produced bark samples), there may be important differences that we were unable to detect. For example, *D. frontalis* was consistently more abundant in the funnel trap samples than in the bark samples, whereas *D. brevicomis* was always more abundant in the samples from the bark compared with the traps (Fig. 5). Galleries of *D. adjunctus* were only recorded in the high-elevation bark samples (Fig. 5A). Likewise, *D. adjunctus* beetles were most abundant in funnel trap samples from high-elevation sites (Fig.

A Model with variables held constant:
Brood tree basal area = 0.29 m²/ha
Elevation x brood tree basal area = 678
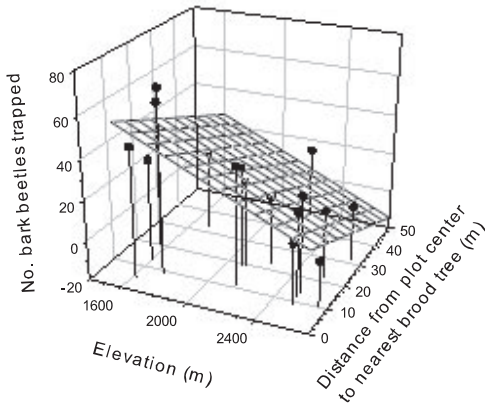
B Model with distance to nearest
brood tree held constant at 18 m
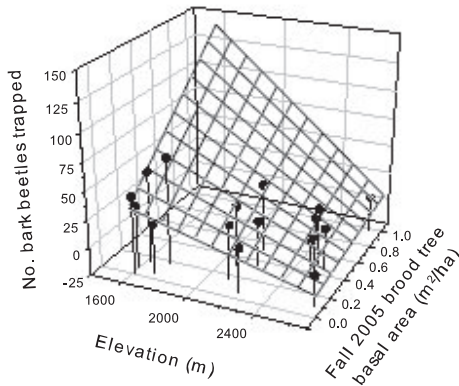
C Model with variables held constant:
Elevation = 2155 m
Elevation x brood tree basal area = 678
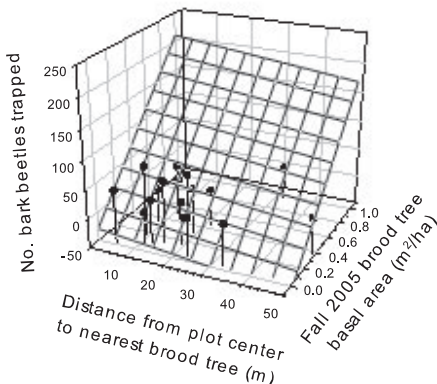
Fig. 3. Three-dimensional multiple regression response surfaces overlaid on the observed data points (solid circles with lines extending down to the bottom plane of the graph) for mean weekly trap catches of all bark beetles at 16 funnel trap sites in north-central Arizona in 2005 (see Table 4C for

5A), and they were barely detectable (0.7%) at the low-elevation sites (Fig. 5C).

Discussion

Relationships between Funnel Trap Catches and Stand and Site Characteristics. Our multiple regression models indicated that both elevation of the funnel trap site and the amount of ponderosa pine in the stand surrounding the trap site had important effects on trap catches. Traps at low-elevation sites that had greater amounts of ponderosa pine captured the most beetles, whereas traps at high-elevation sites that had smaller amounts of ponderosa pine captured the fewest beetles (Figs. 2 and 3B). This suggests that these characteristics should be considered (and quantified, if possible) when locating funnel trap sites. Variation in elevation among trap sites and the amount of host material in the stand should also be considered when interpreting spatial and temporal trends in trap catches, and when prioritizing stands for silvicultural treatments to reduce susceptibility to bark beetles. For example, our results suggest that to reduce stand susceptibility, low-elevation stands would need to have relatively less ponderosa pine compared with higher elevation stands.

The influence of elevation (i.e., elevation gradients) on the diversity and composition of ecological communities has long been recognized (Lomolino 2001). Explanations for differences in species richness, abundance, and diversity due to elevation include climate gradients, isolation of montane communities and reduced area (when higher elevations are found on mountain tops), and feedback among zonal communities (i.e., species density should peak at a transition zone between two species rich communities) (reviewed in Lomolino 2001). Our multiple regression models indicated that elevation of the funnel trap site had important effects on trap catches (i.e., abundance).

We observed a consistent inverse relationship between elevation of the funnel trap site and the number of bark beetles trapped (Figs. 2, 3A and B, and 4A and B). Our results suggest that this inverse relationship is stronger for *Ips* spp. than *Dendroctonus* spp. (Table 3). This corresponds with findings by Williams et al. (2008) that *Dendroctonus* abundance was similar across elevation, whereas *Ips* species were most abundant in the low- and mid-elevation bands. Our results are likely driven by the elevation trends of individual species included in these groups. For example, *I. le-*

the model and statistics). (A) Response surface for elevation and distance from the plot center to the nearest brood tree. (B) Response surface for elevation and percentage of ponderosa pine basal area. (C) Response surface for distance from the plot center to the nearest brood tree and percentage of ponderosa pine basal area. Each panel illustrates the relationship for two of the three independent variables included in the regression model; each response surface was generated by holding the third variable constant at its mean observed value.

A Model with % ponderosa pine basal area held constant at 68%
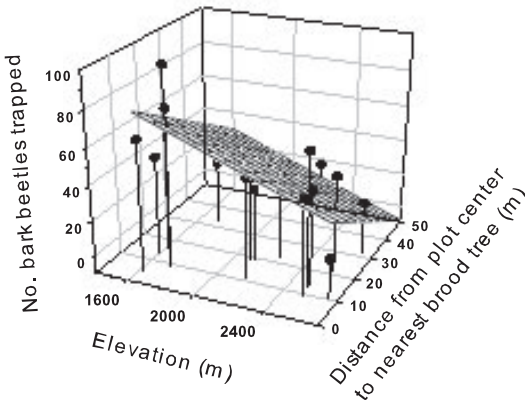
B Model with distance to nearest brood tree held constant at 18 m
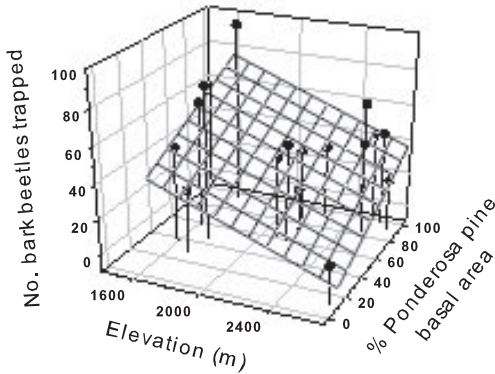
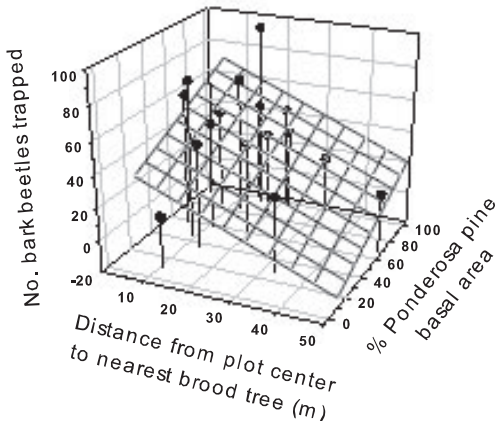## C Model with elevation held constant at 2155 m

Fig. 4. Three-dimensional multiple regression response surfaces overlaid on the observed data points (solid circles with lines extending down to the bottom plane of the graph) for mean weekly trap catches of principal tree-killing bark beetles (*I. lecontei, I. pini. D. brevicomis*, and *D. frontalis*) at

contei and *I. calligraphus* are commonly found at lower elevations (Williams et al. 2008). Alternately, the abundance of *D. frontalis* and *D. brevicomis* at lower elevations is likely offset by the abundance of *D. adjunctus, D. approximatus*, and *D. valens* at higher elevations (Williams et al. 2008), resulting in a weak relationship between *Dendroctonus* sp. and elevation. Additionally, elevation accounted for more variation in the models for "Principal tree-killers" than for the models for "All species" (Table 3). The group "Principal tree-killers" included *I. lecontei. I. pini, D. frontalis*, and *D. brevicomis*, all beetles that are frequently found in the low- and mid-elevation bands (Williams et al. 2008). Conversely, the group "All species" included additional species (*D. adjunctus. D. approximatus*, and *D. valens*) that are most abundant at higher elevations. Consequently, the inverse relationship between elevation and beetle trap catch was stronger in models that used the group "Principal tree-killers" than the group "All species."

Fettig et al. (2005) also reported an inverse relationship between elevation and the number of bark beetles captured in funnel traps in the Sierra Nevada Mountains in California. A highly significant negative correlation coefficient ($r = -0.889, P = 0.003$) was reported for the total number of *D. brevicomis, D. ponderosae* Hopkins, *I. paraconfusus* Lanier, and *I. pini* trapped. For catches of *D. brevicomis*, the correlation was $r = -0.893$ ($P = 0.003$). However, for catches of *I. pini*, the correlation was not significant ($r = 0.658, P = 0.08$). There was a strong inverse relationship between percentage of ponderosa pine in the surrounding stand and elevation, which explained the negative correlation between trap catch and elevation for *D. brevicomis* (Fettig et al. 2005).

In our study, the elevation of the site most likely served as a good composite index of several factors that have direct or indirect influences on bark beetle populations and adult flight activity. Changes in temperature and precipitation associated with changes in elevation influence woody plant communities in terms of species composition, stand density, tree growth rates, and soil moisture (Allen and Breshears 1998). In the arid southwestern United States, higher elevations receive more precipitation compared with lower elevations (Allen and Breshears 1998, Sheppard et al. 2002). Bark beetle larval and pupal development is slowed by lower temperatures, resulting in fewer generations per year (and slower rates of population in-

16 funnel trap sites in north-central Arizona in 2005 (see Table 4D for the model and statistics). (A) Response surface for elevation and distance from the plot center to the nearest brood tree. (B) Response surface for elevation and fall 2005 brood tree basal area, including their interaction. (C) Response surface for distance from the plot center to the nearest brood tree and fall 2005 brood tree basal area. Each panel illustrates the relationship for two of the three independent variables included in the regression model (plus an interaction term if needed); each response surface was generated by holding the third variable constant (and related interaction term) at its mean observed value.
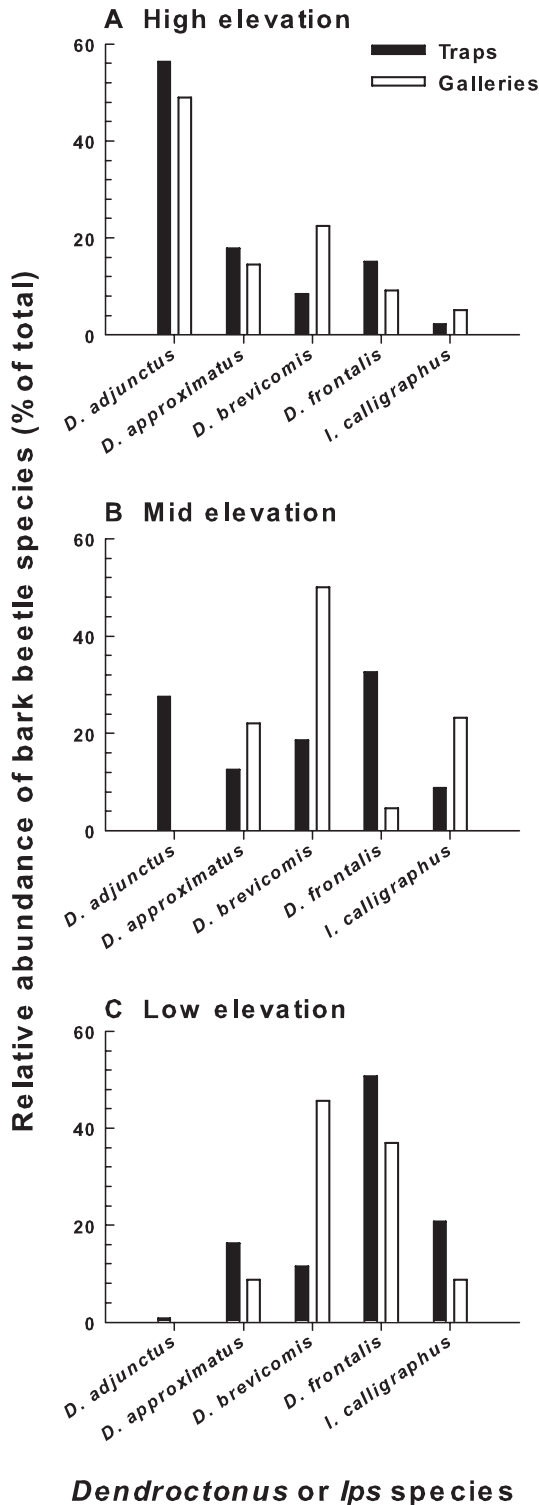
Fig. 5. Relative abundance of four *Dendroctonus* spp. and *I. calligraphus* as determined from funnel trap catches (traps, ■) and bark samples of galleries collected from nearby brood trees (galleries, ☐), for (A) high-, (B) mid-, and (C) low-elevation sites in north-central Arizona in 2005.

crease) for multivoltine species at higher elevations (DeMars and Roettgering 1982, Parker 1991, Hansen 1996, Williams et al. 2008). In addition, bark beetle flight behavior is directly impacted by lower temperatures, because both seasonal and daily degree-day accumulations are lower at higher elevations. Consequently, there is less time during the day and throughout the season when it is warm enough for bark beetles to fly (Gaylord et al. 2008, Williams et al. 2008). Drought stress is more severe at lower elevations in north-central Arizona (Sheppard et al. 2002), and this likely indirectly impacts bark beetle population growth through effects on host tree resistance, which is influenced by tree growth rates and resin flow. Bark beetles that attack ponderosa pines will probably encounter less host tree resistance at lower elevations, especially during prolonged droughts such as the one that has occurred in Arizona since ≈1996 (Adams and Kolb 2004; McPhee et al. 2004; J.D.M., unpublished data). Indeed, Zausen et al. (2005) reported very low rates (<0.1%) of ponderosa pine mortality from bark beetles at mid-elevation (2,160–2,440-m) study sites in northern Arizona from 2003 to 2004, in spite of the widespread mortality from bark beetles that occurred in ponderosa pine forests near the lower extent of their elevational range in Arizona from 2001 to 2003. They attributed this pattern to their study sites being located at higher elevations.

The number of bark beetles captured in funnel traps was positively associated with the amount of ponderosa pine in the stands surrounding the trap sites. Traps located in stands with a greater basal area of ponderosa pine (Fig. 2A) or a greater percentage of ponderosa pine basal area (Figs. 2B and 3B and C) captured more bark beetles. This relationship was expected, given that we were trapping beetles that attack ponderosa pine. The result simply confirms that the beetles already inhabit or tend to be attracted to stands that have more host trees, and this may increase probabilities of trapping beetles in pheromone-baited traps. Positive correlations between stand density and infestation levels have also been observed for *D. adjunctus* in Arizona, New Mexico, and Utah (Negrón 1997, Negrón et al. 2000).

Relatively homogeneous stands with more ponderosa pine would also have lower semiochemical diversity from nonhost tree olfactory cues (Zhang and Schlyter 2004), presumably making it easier for the beetles to locate individual host trees (or artificial pheromone baits) within the stand. Conversely, in stands with high nonhost to host ratios, nonhosts may potentially interfere with beetle host location. This implies that traps should be located in stands with a high ponderosa pine basal area and percentage of ponderosa pine to maximize trap catches. However, in contrast to our findings, Turchin and Odendaal (1996) reported that the efficiency of *D. frontalis* trap catches declined with increased density of host trees around the trap. They suggested that this result may reflect the way *D. frontalis* uses visual cues to locate and land on the closest vertical object when they are in the vicinity of pheromone sources. Thus, a pheromone trap sur-

rounded by many host trees will capture a small proportion of beetles because it provides a weaker visual cue compared with nearby trees (Turchin and Odendaal 1996).

Effect of Distance to the Nearest Brood Tree on Funnel Trap Catches. This variable entered both of our multiple regression models that were developed with the smaller data set of $n = 16$ trap sites (Table 4C and D). Traps located closer to brood trees captured more beetles (Figs. 3A and C and 4A and C). This pattern seemed to be stronger for *Dendroctonus* than for *Ips* species (Table 3); and it may indicate that the majority of emerging *Dendroctonus* adults will not disperse great distances if there are suitable stand conditions and an aggregation pheromone source nearby, whereas *Ips* beetles may have greater dispersal requirements (J.D.M., unpublished data).

When the distance to nearest brood tree is considered simultaneously with elevation and the amount of ponderosa pine, our regression models predict that the highest catches will occur when traps are at low-elevation sites that have a greater percentage of ponderosa pine and brood trees near the trap. Conversely, the lowest catches are predicted to occur at high-elevation sites with a lower percentage of ponderosa pine and when brood trees are not in proximity to the trap. We conclude that it is important to record and consider the presence or absence of brood trees when interpreting trap catch data.

The presence of brood trees near a trap can increase trap catches in several ways. 1) Trees under current attack might provide additional sources of host volatiles and pheromones that increase the overall abundance of bark beetles in the area around the trap; 2) later stage infested trees might provide an additional source of beetles because parent adults reemerge and brood adults emerge later in the flight season or during the subsequent season; and 3) brood trees under current attack and/or baited traps might result in spillover to neighboring trees (Borden 1989, Laidlaw et al. 2003). Given that our funnel traps were deployed at the same sites for the entire beetle flight season in consecutive years, and we used data from the second year of this 3-yr study, it seems that any of these explanations are plausible. Beetles could have spilled over and attacked trees near the traps in 2004 or early in 2005, and then produced pheromones, attracting more beetles into the area and the subsequent generation of beetles that emerged from the nearby spillover trees could have been attracted to the funnel traps later in 2005.

Hansen et al. (2006) defined spillover as infested host trees within 10 m of a funnel trap (by this definition, in 2005 42% of our trapping sites had spillover). They concluded that the absence of spillover was associated with endemic populations of spruce beetles in Engelmann spruce stands in Utah, whereas the presence of spillover was correlated with epidemic conditions. This result suggests that the negative relationship we discovered between distance to the nearest brood tree and trap catches might imply that nearby brood trees, or spillover, occurred more fre-

quently at trap sites that had relatively higher populations of bark beetles in the surrounding stands. If spillover is more frequent when beetle populations are higher, this implies that funnel traps may lead to spot-type attack patterns (groups of attacked trees) during epidemic population phases because there are enough beetles available to overcome the defenses of trees that are attacked near the traps. Beetles might also tend to attack trees near funnel traps during endemic population phases, but they may often be unable to overcome the tree's defenses due to their low numbers.

Do Funnel Trap Catches Track Local Beetle-Induced Tree Mortality? The variable "Fall 2005 brood tree basal area" was not correlated with the number of bark beetles captured for any of the four bark beetle variables that we examined (Table 3); r-values ranged from -0.145–0.134, and the associated P values were ≥ 0.481. In addition, it only entered one of the four multiple regression models that we developed (Table 4D). In this model the regression coefficient was positive; funnel trap sites with a greater basal area of infested trees had higher trap catches (Fig. 4B and C). In addition, there was a significant interaction between this variable and elevation on trap catches; the positive effect that brood tree basal area had on trap catches was greatest at low elevations. Overall, it seems that the relationship between trap catches and host tree mortality in the stands surrounding the funnel traps was relatively weak and inconsistent under the conditions and bark beetle populations examined in our study. These findings suggest that trap catches are poor indicators of localized beetle-induced tree mortality in ponderosa pine stands of the Southwest.

This conclusion is in general agreement with the results from Hansen et al. (2006); they reported a significant positive relationship between spruce beetle trap captures and the number of Engelmann spruce trees killed in the vicinity of a funnel trap, but the relationship was highly variable and model fit was relatively poor. They concluded that funnel-trap captures cannot be used to accurately predict the number of infested spruce trees, although they could provide accurate predictions of whether spruce beetle populations were in epidemic or endemic population phases (Hansen et al. 2006). Funnel trap catches are also used to forecast population trends of *D. frontalis* in the southeastern United States (Billings 1988). In contrast to these studies that can be characterized as having one dominant bark beetle species and hosts grown in less variable stand conditions, the complexity of the bark beetle community inhabiting ponderosa pine in the southwestern United States may make predicting beetle population trends difficult.

Comparison of Bark Beetle Relative Abundance Measured with Funnel Trap Catches Versus Gallery Identification in Bark Samples. Pheromone-baited funnel traps and bark samples from infested trees produced statistically similar relative abundance profiles for the five species of bark beetles that we examined (Fig. 5). This is surprising because the pheromone lures that we used were not specific for four of

the five species that we analyzed; only the lure for *D. brevicomis* was formulated for that particular species. We conclude that the commercial pheromone lures used in this study provided a good assessment of species presence and relative abundance; at each elevation, all of the species found in the bark samples were captured in the funnel traps. In fact, this was true for all the bark beetle species recorded in the bark samples; all nine of the species were also captured in the traps, even though our lures were formulated for only three of them (Table 2).

We were not able to compare the relative abundance profiles for funnel traps versus bark samples for most of the *Ips* species because we only sampled tree bark up to 7 m above the ground, and the majority of *Ips* species tend to attack the higher portions of ponderosa pines (Furniss and Carolin 1977, Kolb et al. 2006, Breece et al. 2008). Thus, although galleries of *I. knausi* and the "other *Ips* species" (*I. latidens, I. lecontei,* and *I. pini*) were present in at least one of the bark samples collected from all four of the bole heights sampled (Table 2), they were not present in enough of the samples to compute reliable abundance profiles. Similarly, the presence of *D. valens* beetles in the funnel traps versus their absence in any of the bark samples (Table 2) reflects their tendency to attack the root collar area of ponderosa pines, at or below ground level (Smith 1971), which is lower on the bole than we sampled.

Finally, we want to note the close association that we observed between *D. brevicomis* and *D. frontalis* in this study. Galleries of these two species were often found together in the same 1,000 cm² of bark. Breece et al. (2008) also observed that 80% of the ponderosa pines attacked by bark beetles in their study sites in Arizona and New Mexico were attacked by more than one species, and 100% of the trees that we sampled had galleries from more than one species. Different species within the species-rich community of bark beetles that attack ponderosa pines in Arizona clearly interact, often sharing not just the same host tree, but the same portion of the bole (Breece et al. 2008).

Acknowledgments

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